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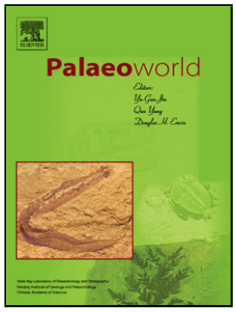

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The Furongian (late Cambrian) Biodiversity Gap: Real or apparent?

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Abstract

Two major, extended diversifications punctuated the evolution of marine life during the Early Palaeozoic. The interregnum, however, between the Cambrian Explosion and the Great Ordovician Biodiversification Event, is exemplified by the Furongian Gap when there was a marked drop in biodiversity. It is unclear whether the gap is apparent, due to sampling failure or lack of rock, or real — associated with unique

and fluctuating environments, a distinctive palaeogeography and extreme climates during the late Cambrian. Indications suggest that there has been little attention paid to this interval compared with those below and above, while some of the classical areas for Cambrian research, such as Bohemia, have poor coverage through the Furongian. Moreover, based on information available in databases and the literature, together with the ghost ranges of many higher taxa through the Furongian, data suggest that biodiversity in this stage has been significantly underestimated. Emphasis, to date, has been placed on widespread, deeper-water dark shale facies of the interval, with generally low diversity faunas, whereas shallow-water communities have often been neglected.

Keywords: Cambrian; GOBE; biodiversity; palaeoenvironments; extinctions; radiations

1. Introduction

The fossil record is probably more gaps than record, expressed a century ago as 'the skimmings of the pot of life' (Huxley, 1862), and noted some decades ago as poorly sampled, with perhaps only 10-15% of genera are known (Boucot, 2000) and poorly taxonomically-studied (Boucot, 1983). Some gaps, for example Romer's Gap in tetrapod evolution during the latest Devonian and Early Carboniferous are being filled by many new body-fossil discoveries (e.g., Clack et al., 2016), exemplifying previous lack of sampling and taxonomic study. The late Cambrian (Furongian) interval is another such biodiversity or evolutionary gap that to date has received comparatively little attention. Did a lack of rock, fossils or inadequate sampling break the continuity between the Cambrian Explosion and the Great Ordovician Biodiversification Event or were conditions simply too inhospitable for marine organisms to flourish?

2. Background

Palaeontologists have long accepted that the fossil record is incomplete but nevertheless adequate to describe and understand the history of life on our planet. Charles Darwin, in his first edition (Darwin, 1859), devoted two chapters to geology and palaeontology in his 'Origin of Species', one 'On the Imperfection of the Geological Record' (chapter nine) and the other 'On the Geological Succession of Organic Beings' (chapter ten). In the first he noted such imperfections do not preserve the entire continuity of life, a 'finely-graduated organic chain', providing a serious objection to the theory of evolution; we thus lack many intermediate and transitional forms. And in the second chapter Darwin highlighted that fossils were generally preserved during intervals of subsidence (increased rates of sedimentation), with blank intervals occurring when the seabed was either stationary or rising. In his summary of the two chapters, Darwin emphasised that only a small portion of the globe had been explored, only specific organisms are preserved as fossils, and that museum collections are an inadequate proxy for the true diversity of the fossil record ('absolutely as nothing as compared with the number of generations which must have passed away even during a single formation'). Nevertheless, old forms were supplanted by new and improved forms as a product of variation and natural selection. One year later John Phillips (1860) published the first comprehensive inventory of fossil range data in his 'Life on Earth'. In his opus, Phillips used the ranges of fossils to define his Palaeozoic, Mesozoic and

Cenozoic eras, portioned by major extinctions and biotic turnovers at the end of the Permian and Cretaceous, respectively. In mapping out the diversity of Phanerozoic life, Phillips noted that more recent formations hosted more diverse biotas than in ancient strata but the abundance of taxa was time-independent. Significantly, and in contrast to Darwin, Phillips considered the imperfections in the fossil record were overrated; in his opinion there are ample fossils to test any hypothesis on the sequence of marine life.

Some hundred years after publication of the 1st edition of Darwin's influential work, interest intensified on the adequacy and quality of the fossil record as more complex and sophisticated analyses of the evolution of fossil organisms and their diversity were developed through deep time. Norman Newell (1959), in his Presidential Address to the Paleontological Society, highlighted the difference between published data and that which is undiscovered and unpublished but knowable information essentially that 'we don't know, what we don't know'. He stressed that lack of data was partly due to inadequate collecting and insufficient preparation techniques to extract fossil material from rock. These and other themes were expanded by a series of influential papers published in the 1970s against a background of debates on the shape of the Phanerozoic biodiversity curve; did it indicate that biodiversity was in equilibrium throughout geological time (Raup, 1972) or expanding (Valentine, 1973)? Raup, in a succession of key papers, developed the concept of time-dependent and time-independent biases (Raup, 1972, 1976a, 1976b). Clearly, outcrop area, thickness and volume of rock has varied throughout geological time with less available for older formations (Raup, 1972, 1976a, 1976b). Moreover, diagenesis, metamorphism and the effects of tectonism are more prevalent in older rocks that have been through orogenic cycles, essentially the primary rocks of Giovanni Arduino (1760). As a result these rocks, commonly in the world's mountain belts, have been less explored for fossils than say the younger, more pristine strata. There are a range of biases that are not time dependent. There are errors in dating the length of units, biotic turnover rates are unpredictable, preservation is variable across the phyla, sedimentary facies are unevenly developed through time and their monographic effects (Raup, 1972, 1976a, 1976b). Sheehan (1977) developed the last argument, noting that there were areas of palaeontological interest, where the focus of a specialist or groups of specialists can markedly enhance diversity by intensive monographic description. Some of these key themes had already been signalled by Raup and Stanley (1971) in their game-changing textbook; touched on subsequently in its third edition (Foote and Miller, 2007).

Nevertheless Benton et al. (2000), through an analysis of the correspondence of phylogenetic trees with the fossil record, demonstrated the fit was equally good whether dealing with Palaeozoic groups or taxa in the Cenozoic.

There is clearly a close relationship between the fossil and rock records. Smith (2001) demonstrated that, over the last 600 myr, diversity tracked sea level in general terms; preservation of taxa was usually low during regressive intervals and high during transgressions. However, McGowan and Smith (2008) noted that global eustatic curves may not be a good proxy for outcrop area; actual regional data on rock occurrence may provide a better signal. Whereas Peters and Foote (2002) emphasised a correlation between named formations and named fossils; rather the appearance and disappearance of fossils may be linked to the presence and absence of strata. An implication being that geology is actually controlling preserved biodiversity, framing the preservation bias hypothesis. It is, however, plausible that the signal is real. Peters' (2005) common cause hypothesis posited that during intervals of high sea level biodiversity is actually high and during regression it drops (see also Hannisdal and Peters, 2012). Transgressions provide not only increased habitable areas for marine biotas but also an increased volume of fossiliferous rock. There remain vast areas of Furongian rocks that have not be adequately explored or not explored at all, particularly across eastern parts of Gondwana; nearshore environments, the probable origin of many clades, have been especially neglected. These key factors may provide some explanation for the current dearth of data from this critical interval.

3. The Furongian record

The Furongian Series consists of three stages, the Paibian, Jiangshanian and Stage 10, of 3, 4.5 and 4 myr duration, respectively. The Furongian fossil record is poorly known (Fig. 1). It is, however, constrained between two segments of the stratigraphical column exhibiting prominent levels of biodiversity. The Cambrian Explosion, massively enhanced by a number of key Lagerstätten, is a topic of extreme taxonomic interest (Erwin and Valentine, 2013; Briggs, 2015), although represented by relatively few formations, with restricted areas of outcrop and thickness; moreover, a number of the Cambrian Lagerstätten, e.g., Burgess Shale and Sirius Passet, were subject to diagenesis, metamorphism and the effects of tectonism. Diversity of higher taxa is marked though represented by relatively few taxa at lower taxonomic levels such as families, genera and species. By contrast, the Great Ordovician Biodiversification

Event (GOBE) is underpinned by a massive increase in diversity at the lower taxonomic levels (Harper, 2006; Rong et al., 2007; Harper and Servais, 2018), commonly apparent across clastic and limestone facies initially on shallow shelves. The lack of data, if real, may firstly serve to partition the rise of diversity during the Cambrian and Ordovician into two discrete but ostensibly different events; but if lack of data is apparent, this would favour a single trajectory for both events peaking during the Devonian, as illustrated for example by Alroy et al. (2008, fig. 4) and Alroy (2010, fig. 3).

The palaeogeography of the Furongian is also distinctive (Álvaro et al., 2007). Faunas are best known from black shale belts and shallow-water carbonates (Fig. 2), both hosting more specialised and commonly endemic faunas. The distribution patterns of the faunas adds a further restriction on the mapping and understanding of global diversity during this epoch and of course provides a further constraint on available fossiliferous rock.

Apart from personal knowledge, we are reliant on three key sources of information, Sepkoski's database (see http://strata.geology.wisc.edu/jack/), the Paleobiology Database (PBDB: see https://paleobiodb.org/#/) and the Geobiodiversity Database (GBDB: http://www.geobiodiversity.com/). All three databases indicate the record is far from complete.

4. Fact or artefact?

Furongian rocks are known from all major Cambrian palaeocontinents and widely distributed in many regions, such as in Laurentia, South China, Siberia and Baltica. In other regions, the Furongian Series is sporadically distributed and restricted to a few lithofacies belts. This is true for a number of classic areas of Cambrian research from western Gondwana, for example the Barrandian area of Bohemia, Spain and Morocco, together with parts of the Baltic (e.g., Estonia) where the Furongian is poorly represented or consists of shallow-water deposits that are poorly fossiliferous. Thus, the lack of continuity of sections in some of the world's classic, and intensively-investigated areas for Cambrian rocks has clearly contributed to the gap.

To test both scenarios, diversity data was plotted together with sampling signals and to evaluate the fit between both time series. A comprehensive genus-level dataset was downloaded from the Paleobiology Database (PBDB), comprising 206,560 fossil occurrences ranging from Cambrian to lowermost Devonian (raw download available in supplementary material). Both marine and terrestrial data were included. All

lithologies were considered. No filter was used. Data analysis was carried out at the stage-level, i.e., 26 time bins. From this, we obtained, as raw parameters, the four fundamental categories of taxa for a given stage bin (Foote, 2000, fig. 1), as well as the sampled-in-bin (SIB) diversity and the number of occurrences considered in each case. Total and boundary-crossing (BC) standing diversity, i.e., the initial diversity of each interval, were also calculated. SIB diversity and the occurrence richness were considered as proxies of sampling effort. A direct comparison of diversity and sampling signal against time show that overall, the apparent observed patterns of PBDB diversity is driven by sampling, which is especially significant in the Cambrian, e.g., concerning total diversity. In fact, total and SIB diversity follow comparable trajectories, which seems to fit to occurrence signal, while BC diversity reflects an independent pattern (Fig. 1). As such, we tested the relationship between total and BC diversity patterns and the sampling pattern per stage bin. The parametric Pearson (r), and non-parametric Spearman (r_s) and Kendall (t) correlation tests were used (see Hammer and Harper, 2006). To avoid inconsistences generated by false positives, we ran a two-time data analysis from raw and generalized-differenced (detrended) data for comparisons (see http://www.graemetlloyd.com/methgd.html for implementation). Using a significance level of 1%, total and SIB diversity provided highly significant results in all cases (Table 1). Identical results were obtained between the total and SIB diversity and occurrences (Table 1). Despite raw data analysis of BC diversity and sampling signal providing slightly significant values (in comparison to previous cases), detrended data analysis of BC diversity and sampling signal did not show significant correlated values (Table 1). Evidence seems to suggest that, the overall observed diversity (in particular total diversity) may be driven by sampling, sampling does not account for the entire diversity signal; a biological signal is still legible in the fossil record.

5. Natural causes

Diversity curves based on the Sepkoski Database indicate a high frequency of extinctions during the late Cambrian (Fig. 3). The frequency and magnitude of these events, especially when displayed as proportions of extinct genera, are impressive (see e.g., Melott and Bambach, 2012; Erlykin et al., 2018). Nevertheless sample sizes are relatively small and fluctuations when present may appear disproportionately large.

The Furongian was an interval of substantial changes in palaeoceanographic conditions that may have influenced the patterns of biogeography, evolution, faunal

turnovers and extinctions (e.g., Saltzman et al., 2000; Peng et al., 2004; Kouchinsky et al., 2008; Ahlberg et al., 2009; Dahl et al., 2014). Although in its infancy, palaeoceanography research in the Cambrian has provided evidence for thermally stratified oceans and a distinct temperature gradient from higher to lower latitudes, dramatic sea-level changes, and time intervals of dysoxia or anoxia during parts of the Furongian (e.g., Gill et al., 2011; Babcock et al., 2015; Saltzman et al., 2015 and references therein). There are no unambiguous evidence for glaciations during the Furongian, but studies that hint at, or provide some evidence, for the possibility of extensive Cambrian glaciations were briefly reviewed by Babcock et al. (2015). These studies include papers describing the evidence for a permanent thermocline (Taylor and Cook, 1976; Cook and Taylor, 1977; Taylor and Forester, 1979) and cold water impinging on the shallow tropical seas of Laurentia at the end-biomere extinctions (Stitt, 1975; Perfetta et al., 1999; Taylor, 2006; Runkel et al., 2010).

Two globally significant carbon isotope excursions are recognized in the Furongian, the Steptoean Positive carbon Isotope Excursion (SPICE) in the Paibian Stage and the HEllnmaria — Red Tops Boundary Event (HERB) or Top of Cambrian Excursion (TOCE) in provisional Stage 10 (Zhu et al., 2006; Fig. 3 herein). Both excursions are indicative of perturbations in the oceanic carbon cycle, and can be used to recognize major physico-chemical and biological changes in the world ocean (e.g., Ripperdan et al., 1992; Saltzman et al., 2000, 2004; Miller et al., 2015). The onset of the SPICE is associated with the base of the Furongian Series (Peng et al., 2004), whereas the HERB event (or TOCE) occurs near the top of the Cambrian (e.g., Miller et al., 2014, 2015). The SPICE has an amplitude of up to +5‰ in the $\delta^{13}C_{carb}$ values (Fig. 3) and lasted for 2–4 Ma (Saltzman et al., 2000, 2004; Kouchinsky et al., 2008; Woods et al., 2011; Barili et al., 2018). The HERB Event (TOCE) is a high-amplitude negative excursion with a net shift of ca. –2 to –5‰ in the $\delta^{13}C_{carb}$ values (Fig. 3). The SPICE and HERB events have also been recognized in $\delta^{13}C_{org}$ curves from shale successions (Ahlberg et al., 2009, in press; Saltzman et al., 2011; Woods et al., 2011; Terfelt et al., 2014; Hammer and Svensen, 2017). The magnitude of the SPICE and the HERB Event in shale successions is, however, subdued compared to the $\delta^{13}C_{carb}$ excursions recorded in carbonate successions, and the $\delta^{13}C_{org}$ signal is commonly half, or less than half, of the magnitude the $\delta^{13}C_{carb}$ signal (see Ahlberg et al., in press and references therein).

The cause(s) of the major carbon-cycle perturbations evidenced by the SPICE and HERB events is not well understood, but can probably be related to sea-level changes, the degree of oceanic stratification and oxygen deficiency, and the rate of nutrient discharge, biological productivity and/or continental weathering of marine carbonates.

Organic-rich dark to black shales and dark grey to black limestone-shale successions are particularly well-known from many Furongian shelf, slope and basinal environments. Some of the best examples of Furongian organic-rich deposits are in South China, Baltica (notably Scandinavia) and Avalonia (e.g., southern Britain, New England and Atlantic Canada). These deposits reflect enhanced organic matter burial and suggest that oxygen deficiency was widespread in subsurface water masses in the Furongian (Gill et al., 2011; Saltzman et al., 2015). The SPICE event has been characterised as the best anoxic event recorded for pre-Mesozoic oceans and the episodic expansion of depleted bottom waters may have had a dominant influence on the development of marine animals at a critical time in metazoan evolution (Gill et al., 2011). The interpretation of the SPICE as a global anoxic event has, however, been questioned, because the presence of benthic faunal elements and bioturbation in almost all SPICE-related sections excludes widespread and persistent anoxia or euxinia, but rather suggest oxic or dysoxic sea floor conditions during most of the SPICE interval (Egenhoff et al., 2015; Wotte and Strauss, 2015). Geochemical evidence also indicates that there was a major increase in atmospheric oxygen in the Furongian, and that the SPICE event was followed by an increase in primary productivity that may relate to changes in the abundance of nutrients in increasingly oxic marine environments (Saltzman et al., 2011), possibly triggering the 'Ordovician Plankton Revolution' (Servais et al., 2016). In most regions, the SPICE can be associated with sea-level oscillations and it is presumed to have been initially triggered by a sea-level rise that brought oxygen-deficient waters onto the shelves (Gill et al., 2011). Most of this $\delta^{13}C$ excursion, however, including the peak, seems to be in an interval of eustatic fall that likely resulted in compression of shelf habitats (e.g., Woods et al., 2011; Babcock et al., 2015; Saltzman et al., 2015; Fig. 3 herein). Thus, this low stand may have had an intrinsic impact on the preserved record of Furongian evolutionary history.

The HERB (or TOCE) Event has been identified in a number of regions on widely separate palaeocontinents and can be used for global correlation of uppermost Cambrian strata. There is, however, no general consensus for the cause of this major negative excursion, but it may be linked to eustatic sea-level changes that influenced

oceanic redox conditions and hence the primary organic production (Azmy, in press and references therein).

The concept of biomeres was introduced over 50 years ago (see Palmer, 1984 and Taylor, 2006 for reviews). These trilobite-based evolutionary units, first recognized in Laurentia, included several biozones and are sharply delimited by extinction events. Biomere boundaries have subsequently been shown to coincide with major faunal turnovers on other palaeocontinents, such as Australia, South China and Baltica (Saltzman et al., 2000; Peng et al., 2004; Ahlberg et al., 2009; Babcock et al., 2017 and references therein). Palmer (1984) considered the extinction events may be associated with a rapid rise in the thermocline or widespread anoxia. The increasing evidence for a anoxia/dysoxia (e.g., Gill et al., 2011) apparently supports the latter hypothesis, but, as reviewed by Taylor (2006), there is also geological evidence consistent with relative sea-level rise and water temperature decline at biomere boundaries (see also Babcock et al., 2015).

Three late Cambrian extinctions have been correlated with biomere boundaries, associated with $\delta^{13}C$ excursions, sea-level change and the spread of anoxia (for data see Saltzman et al., 2015). The combination of positive excursions of $\delta^{13}C$ and $\delta^{34}S$ signalled the spread of anoxia and dysoxia across the shelves invoking invoking changes in the habitat structure that contributed extinctions and a decreased diversity particularly amongst the benthos; changes in ocean circulation and ventilation impacted on the deeper-water ecosystem.

These observations have formed the basis for hypotheses implicating oxygen as a driver for the GOBE. With rising oxygen the ocean cooled and increased oxygen would enable the evolution of larger animals with thicker skeletons and provide for an enhanced arms race as increased weaponry was matched by increased armour together with innovative avoidance and evasive strategies. Cooler surface waters and higher oxygen levels were key to these transformations (Edwards et al., 2017).

Nevertheless these events may not be synchronous or even globally pervasive. Schiffbauer et al. (2017) have suggested that the SPICE event is possibly time transgressive and potentially facies dependent, and Barili et al. (2018) noted that the SPICE may locally reflect superposition of a regional and local carbon isotopic signature onto ocean chemistry.

These events not only affected the macrofauna but trace fossils imply that behavioural patterns were also changing. Macroborers are relatively rare through the

Furongian although Lee et al. (2018) have recently reported *Trypanites* and forms similar to *Gastrochoenolites* from flat-pebble conglomerates, marking a recovery in the ichnofauna of hard grounds following the demise of the archaeocyathan-microbialite reef ecosystem.

6. Conclusions

Currently there is marked interregnum in biodiversity between the high-profile, exceptionally-preserved biotas of the Cambrian Explosion, preserved across a number of Lagerstätten, and the four-fold increase in numbers of families, genera and species during the Great Ordovician Biodiversification Event. Is the gap real, i.e., is there a clear partition between two events, or is this merely apparent? The latter presenting the intriguing possibility that the diversification of marine ecosystems was on a single trajectory that peaked in the Devonian. Understanding the Furongian Gap is a critical test of both hypotheses.

1. There is limited data available in the key biodiversity and lithological databases, particularly the PBDB, that are routinely used for modelling Phanerozoic biodiversity.
2. This may in part be due to a relative lack of adequate fossiliferous strata through this key interval, and the disappearance of Konservat-Lagerstätten.
3. Facies belts largely restricted to black shales or shallow-water carbonate facies, generally host more specialised and less widespread faunas.
4. There are relatively few fossil collections, compared with older and younger strata, through this interval coupled with a lack of taxonomic work on its biotas.
5. Extreme fluctuations are present in Furongian environments, providing a barrier to the expansion of the marine ecosystem and its biodiversity.

In summary, in addition to inadequate sampling, fluctuating conditions, particularly between those of anoxia and dysoxia at biomere boundaries would have retarded any acceleration in biodiversity. That had to wait until the Early Ordovician.

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References

Ahlberg, P., Axheimer, N., Babcock, L.E., Eriksson, M.E., Schmitz, B., Terfelt, F., 2009. Cambrian high-resolution biostratigraphy and carbon isotope chemostratigraphy in Scania, Sweden: first record of the SPICE and DICE excursions in Scandinavia. Lethaia 42, 2–16.

Ahlberg, P., Lundberg, F., Erlström, M., Calner, M., Lindskog, A., Dahlqvist, P., Joachimski, M.M., in press. Integrated Cambrian biostratigraphy and carbon isotope chemostratigraphy of the Grönhögen-2015 drill core, Öland, Sweden. Geological Magazine, doi: 10.1017/S0016756818000298.

Alroy, J., 2010. The shifting balance of diversity among major marine animal groups. Science 329, 1191–1994.

Alroy, J., Aberhan, M., Bottjer, D.J., Foote, M., Fürsich, F.T., Harries, P.J., Hendy, A.J., Holland, S.M., Ivany, L.C., Kiessling, W., Kosnik, M.A., Marshall, C.R., McGowan, A.I., Miller, A.I., Olszewski, T.D., Patzkowsky, M.E., Peters, S.E., Villier, L., Wagner, P.J.., Bonuso, M., Borkow, P.S., Brenneis, B., Clapham, M.E., Fall, L.M., Ferguson, C.A., Hanson, V.L., Krug, A.Z., Layou, K.M., Leckey, E.H., Nürnberg, S., Powers, C.M., Sessa, J.A., Simpson, C., Tomašových, A., Visaggi., C.C., 2008. Phanerozoic trends in the global diversity of marine invertebrates. Science 321, 97–100.

Álvaro, J.J., Ferretti, A., González-Gómez, C., Serpagli, E., Totello, F., Vecoli, M., Vizcaïno, D., 2007. A review of the Late Cambrian (Furongian) palaeogeography in the western Mediterranean region, NW Gondwana. Earth-Science Reviews 85, 47–81.

Arduino, G., 1760. Lettera Segonda di Giovanni Arduino … sopra varie sue osservazioni fatte in diverse parti del territorio di Vicenza, ed altrove, apparenenti alla Teoria terrestre, ed alla Mineralogia [Second letter of Giovanni Arduino … on his various observations made in different parts of the territory of Vincenza, and elsewhere, concerning the theory of the earth and mineralogy]. Nuova Raccolta d'Opuscoli Scientifici e Filologici [New Collection of Scientific and Philogical Pamphlets] 6, 133 (cxxxiii)–180 (clxxx) (in Italian).

Azmy, K., in press. Carbon-isotope stratigraphy of the uppermost Cambrian in eastern Laurentia: implications for global correlation. Geological Magazine, doi: 10.1017/S001675681800002X.

Babcock, L.E., Peng, S.C., Brett, C.E., Zhu, M.Y., Ahlberg, P., Bevis, M., Robison, R.A., 2015. Global climate, sea-level cycles, and biotic events in the Cambrian Period. Palaeoworld 24, 5–15.

Babcock, L.E., Peng, S.C., Ahlberg, P., 2017. Cambrian trilobite biostratigraphy and its role in developing an integrated history of the Earth system. Lethaia 50, 381–399.

Barili, R., Neilson, J.E., Brasier, A.T., Goldberg, K., Bardola, T.P., de Ros, L.F., Leng, M., 2018. Carbon isotopes, stratigraphy, and environmental change: the Middle–Upper Cambrian Positive Excursion (SPICE) in Port au Port Group, western Newfoundland, Canada. Canadian Journal of Earth Sciences 55 (11), 1209–1222.

Benton, M.J., Wills, M.A., Hitchin, R., 2000. Quality of the fossil record through time. Nature 403, 534–537.

Bergström, S.M., Chen, X., Gutiérrez-Marco, J.C., Dronov, A., 2009. The new chronostratigraphic classification of the Ordovician System and its relations to major regional series and stages and to $\delta^{13}C$ chemostratigraphy. Lethaia 42, 97–107.

Boucot, A.J., 1983. Does evolution take place in an ecological vacuum? II. "*The time has come the Walrus said...*" Journal of the Paleontological Society 57, 1–30.

Boucot, A.J., 2000. Presentation of the Palaeontological Society Medal to Arthur J. Boucot. Response by Arthur J. Boucot. Journal of Paleontology 74, 756–757.

Briggs, D.E.G., 2015. The Cambrian Explosion. Current Biology 25, R864–R868.

Clack, J.A., Bennett, C.E., Carpenter, D.K., Davies, S.J., Fraser, N.C., Kearsey, T.I., Marshall, J.E.A., Millward, D., Otoo, B.K.A., Reeves, E.J., Ross, A.J., Ruta, M., Smithson, K.Z., Smithson, T.R., Walsh, S.A., 2016. Phylogenetic and environmental context of a Tournaisian tetrapod fauna. Nature Ecology & Evolution 1, Article number 0002, doi: 10.1038/s41559-016-0002.

Cook, H.E., Taylor, M.E., 1977. Comparison of continental slope and shelf environments in the Upper Cambrian and lowest Ordovician of Nevada. In: Cook, H.E., Enos, P. (Eds.), Deep-Water Carbonate Environments. Society of Economic Paleontologists and Mineralogists, Special Publication 25, 51–81.

Dahl, T.W., Boyle, R.A., Canfield, D.E., Connelly, J.N., Gill, B.C., Lenton,T.M., Bizzarro, M., 2014. Uranium isotopes distinguish two geochemically distinct stages during the later Cambrian SPICE event. Earth and Planetary Science Letters 402, 313–326.

Darwin, C., 1859. On the Origin of Species by Means of Natural Selection, or the Preservation of Favoured Races in the Struggle for Life. John Murray, London, 502 pp.

Edwards, C.T., Fike, D.A., Saltzman, M.R., Lu, W.Y., Lu, Z.L., 2017. Evidence for local and global redox conditions at an Early Ordovician (Tremadocian) mass extinction. Earth and Planetary Science Letters 481, 125–135.

Egenhoff, S.O., Fishman, N.S., Ahlberg, P., Maletz, J., Jackson, A., Kolte, K., Lowers, H., Mackie, J., Newby, W., Petrowsky, M., 2015. Sedimentology of SPICE (Steptoean positive carbon isotope excursion): A high-resolution trace fossil and microfabric analysis of the middle to late Cambrian Alum Shale Formation, southern Sweden. The Geological Society of America, Special Paper 515, 87–102, doi: 10.1130/2015.2515(05).

Erlykin, A., Harper, D.A.T., Sloan, T., Wolfendale, A., 2018. Periodicity in extinction rates. Palaeontology 61, 149–158.

Erwin, D., Valentine, J., 2013. The Cambrian Explosion: The Construction of Animal Biodiversity. W.H. Freeman, New York, 416 pp.

Foote, M., 2000. Origination and extinction components of taxonomic diversity: general problems. Palaeobiology 26, 74–102.

Foote, M., Miller, A., 2007. Principles of Paleontology. 3rd Edition. W.H. Freeman, New York, 354 pp.

Gill, B.C., Lyons, T.W., Young, S.A., Kump, L.R., Knoll, A.H., Saltzman, M.R., 2011. Geochemical evidence for widespread euxinia in the later Cambrian ocean. Nature 469, 80–83.

Hammer, Ø., Harper, D.A.T., 2006. Paleontological Data Analysis. Blackwell Publishing, Oxford. 351 pp.

Hammer, Ø., Svensen, H.H., 2017. Biostratigraphy and carbon and nitrogen geochemistry of the SPICE event in Cambrian low-grade metamorphic black shale, southern Norway. Palaeogeography, Palaeoclimatology, Palaeoecology 468, 216–227.

Hannisdal, B., Peters, S., 2012. Phanerozoic Earth system evolution and marine biodiversity. Science 334, 1121–1124.

Harper, D.A.T., 2006. The Ordovician biodiversification: Setting an agenda for marine life. Palaeogeography, Palaeoclimatology, Palaeoecology 232, 14–166.

Harper, D.A.T., Servais, T. (Eds.), 2018. Contextualizing the onset of the Great Ordovician Biodiversification Event. Lethaia 51, 149–323.

Haq, B.U., Schutter, S.R., 2008. A chronology of Palaeozoic sea-level changes. Science 322, 64–68.

Huxley, T.H., 1862. In correspondence with Charles Darwin, May 6th 1982. University of Cambridge, www.darwinproject.ac.uk/letter/DCP-LETT-3535.xml.

Kouchinsky, A., Bengtson, S., Gallet, Y., Korovnikov, I., Pavlov, V., Runnegar, B., Shields, G., Veizer, J., Young, E., Ziegler, K., 2008. The SPICE carbon isotope excursion in Siberia: a combined study of the upper Middle Cambrian–lowermost Ordovician Kulyumbe River section, northwestern Siberian Platform. Geological Magazine 145, 609–622.

Lee, J.-H., Choh, S.-J., Lee, D.-J., 2018. Late Cambrian missing link in macroborer evolution preserved in intraclasts. Palaeogeography, Palaeoclimatology, Palaeoecology 489, 137–146.

McGowan, A.J., Smith, A.B., 2008. Are global Phanerozoic marine diversity curves truly global? A study of the relationship between regional rock records and global Phanerozoic marine diversity. Paleobiology 34, 80–103.

Melott, A.L., Bambach, R.K., 2012. Analysis of periodicity using 2012 geological timescale. Palaeobiology 40, 177–196.

Miller, J.F., Evans, K.R., Freeman, R.L., Ripperdan, R.L., Taylor, J.F., 2014. The proposed GSSP for the base of Cambrian Stage 10 at the First Appearance Datum of the conodont *Eoconodontus notchpeakensis* (Miller, 1969) in the House Range, Utah, USA. GFF 136, 189–192.

Miller, J.F., Ripperdan, R.L., Loch, J.D., Freeman, R.L., Evans, K.R., Taylor, J.F., Tolbart, Z.C., 2015. Proposed GSSP for the base of Cambrian Stage 10 at the lowest occurrence of *Eoconodontus notchpeakensis* in the House Range, Utah, USA. Annales de Paléontologie 101, 199–211.

Munnecke, A., Calner, M., Harper, D.A.T., Servais, T., 2010. Ordovician and Silurian sea-water chemistry, sea level, and climate: A synopsis. Palaeogeography, Palaeoclimatology, Palaeoecology 296, 389–413.

Newell, N.D., 1959. Adequacy of the fossil record. Journal of Paleontology 33, 488–499.

Palmer, A.R., 1984. The biomere problem: Evolution of an idea. Journal of Paleontology 58, 599–611.

Peng, S.C., Babcock, L.E., Robison, R.A., Lin, H.L., Rees, M.N., Saltzman, M.R., 2004. Global Standard Stratotype-section and Point (GSSP) of the Furongian Series and Paibian Stage (Cambrian). Lethaia 37, 365–379.

Perfetta, P.J., Shelton, K.L., Stitt, J.H., 1999. Carbon isotope evidence for deep-water invasion at the Marjumiid-Pterocephaliid biomere boundary, Black Hills, USA. Geology 27, 403–406.

Peters, S., 2005. Geologic constraints on the macrevolutionary history of marine animals. Proceedings of the National Academy of Sciences of the United States of America 102, 12326–12331.

Peters, S., Foote, M., 2002. Determinants of extinction in the fossil record. Nature 416, 420–424.

Phillips, J., 1860. Life on Earth: Its Origin and Succession. Macmillan and Co., Cambridge, 224 pp.

Raup, D., 1972. Taxonomic diversity during the Phanerozoic. Science 177, 1065–1071.

Raup, D., 1976a. Species diversity in the Phanerozoic: a tabulation. Paleobiology 2, 279–288.

Raup, D., 1976b. Species diversity in the Phanerozoic: an interpretation. Paleobiology 2, 289–297.

Raup, D.M., Stanley, S.M., 1971. Principles of Paleontology. W.H. Freeman, San Francisco, 388 pp.

Ripperdan, R.L., Magaritz, M., Nicoll, R.S., Shergold, J.H., 1992. Simultaneous changes in carbon isotopes, sea level, and conodont biozones within the Cambrian–Ordovician boundary interval at Black Mountain, Australia. Geology 20, 1039–1042.

Rong, J.Y., Fan, J.X., Miller, A.I., Li, G.X., 2007. Dynamic patterns of latest Proterozoic–Palaeozoic–early Mesozoic marine biodiversity in South China. Geological Journal 42, 431–454.

Runkel, A.C., Cowan, C.A., Fox, D.L., 2010. Tropical shoreline ice in the late Cambrian: implications for Earth's climate between the Cambrian Explosion and the Great Ordovician Biodiversification Event. GSA Today 20 (11), 4–10.

Saltzman, M.R., Ripperdan, R.L., Brasier, M.D., Lohmann, K.C., Robison, R.A., Chang, W.T., Peng, S.C., Ergaliev, E.K., Runnegar, B., 2000. A global carbon isotope excursion (SPICE) during the Late Cambrian: relation to trilobite extinctions, organic-matter burial and sea level. Palaeogeography, Palaeoclimatology, Palaeoecology 162, 211–223.

Saltzman, M.R., Cowan, C.A., Runkel, A.C., Runnegar, B., Stewart, M.C., Palmer, A.R., 2004. The Late Cambrian SPICE ($\delta^{13}C$) event and the Sauk II–Sauk III regression: new evidence from Laurentian basins in Utah, Iowa, and Newfoundland. Journal of Sedimentary Research 74, 366–377.

Saltzman, M.R., Young, S.A., Kump, L.R., Gill, B.C., Lyons, T.W., Runnegar, B., 2011. Pulse of atmospheric oxygen during the late Cambrian. Proceedings of the National Academy of Sciences of the United States of America 108, 3876–3881.

Saltzman, M.R., Edwards, C.T., Adrain, J.M., Westrop, S.R., 2015. Persistent anoxia and elevated extinction rates separate the Cambrian and Ordovician radiations. Geology 43, 808–810.

Schiffbauer, J.D., Huntley, J.W., Fike, D.A., Jeffrey, M.J., Gregg, J.M., Shelton, K.L. 2017. Decoupling biogeochemical records, extinction, and environmental change during the Cambrian SPICE event. Science Advances 3 (3), e1602158, doi: 10.1126/sciadv.1602158.

Servais, T., Perrier, V., Danelian, T., Klug, C., Martin, R., Munnecke, A., Nowak, H., Nützel, A., Vandenbroucke, T.R.A., Williams, M., Rasmussen, C.M.Ø., 2016. The onset of the 'Ordovician Plankton Revolution' in the late Cambrian. Palaeogeography, Palaeoclimatology, Palaeoecology 458, 12–28.

Sheehan, P.M., 1977. A reflection of labor by systematists? Paleobiology 3, 325–329.

Smith, A., 2001. Large-scale heterogeneity of the fossil record: implications for Phanerozoic biodiversity studies. Philosophical Transactions of the Royal Society B 356, 351–367.

Stitt, J.H., 1975. Adaptive radiation, trilobite paleoecology and extinction, Ptychaspidid Biomere, Late Cambrian of Oklahoma. Fossils and Strata 4, 381–390.

Taylor, J.F., 2006. History and status of the biomere concept. Memoirs of the Association of Australasian Palaeontologists 32, 247–265.

Taylor, M.E., Cook, H.E., 1976. Continental shelf and slope facies in the Upper Cambrian and lowest Ordovician of Nevada. Brigham Young University Geology Studies 23 (2), 181–214.

Taylor, M.E., Forester, R.M., 1979. Distributional model for marine isopod crustaceans and its bearing on early Paleozoic paleozoogeography and continental drift. Geological Society of America Bulletin 90, 405–413.

Terfelt, F., Eriksson, M.E., Schmitz, B., 2014. The Cambrian–Ordovician transition in dysoxic facies in Baltica — diverse faunas and carbon isotope anomalies. Palaeogeography, Palaeoclimatology, Palaeoecology 394, 59–73.

Valentine, J., 1973. Phanerozoic taxonomic diversity: a test of alternate models. Science 180, 1078–1079.

Woods, M.A., Wilby, P.R., Leng, M.J., Rushton, A.W.A., Williams, M., 2011. The Furongian (late Cambrian) Steptoean Positive Carbon Isotope Excursion (SPICE) in Avalonia. Journal of the Geological Society, London 168, 851–861.

Wotte, T., Strauss, H., 2015. Questioning a widespread euxinia for the Furongian (Late Cambrian) SPICE event: indications from $\delta^{13}C$, $\delta^{18}O$, $\delta^{34}S$ and biostratigraphic constraints. Geological Magazine 152, 1085–1103.

Zhu, M.Y., Babcock, L.E., Peng, S.C., 2006. Advances in Cambrian stratigraphy and paleontology: integrating correlation techniques, paleobiology, taphonomy and paleoenvironmental reconstruction. Palaeoworld 15, 217–222.

Figure captions

Fig. 1. Comparison of PBDB genus-level diversity (A) with PBDB genus-level occurrences (B).

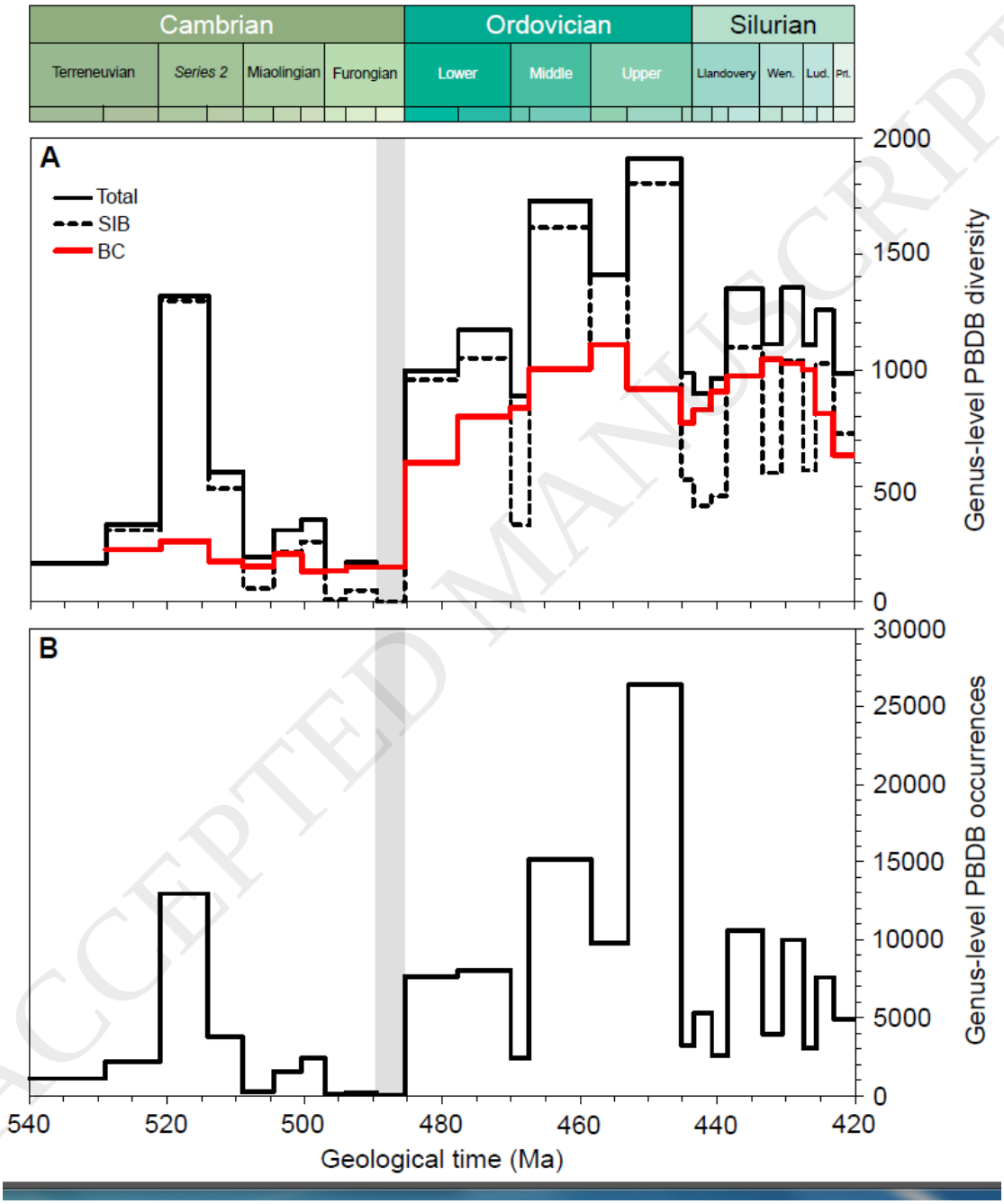

Fig. 2. The palaeogeography of the Furongian Epoch, highlighting the distribution of black shale facies and shallow-water carbonates (modified from Álvaro et al., 2007).

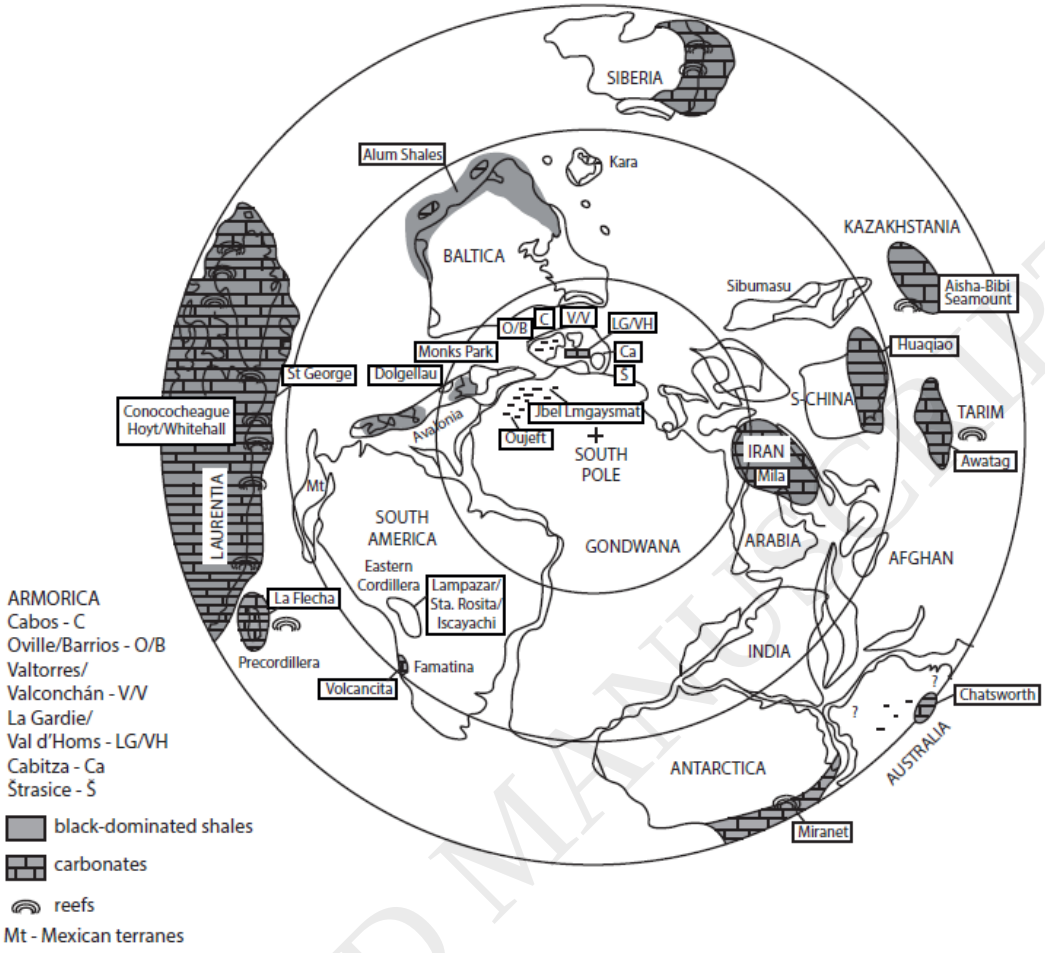

Fig. 3. Genus-level diversity, proportion of extinction (based on data in the PBDB) together with carbon isotope and sea-level data through the Lower Palaeozoic (replotted from Zhu et al., 2006, fig. 1; Haq and Schutter, 2008, figs. 1 and 2; Bergström et al., 2009, fig. 2; Munnecke et al. 2010, fig. 4).

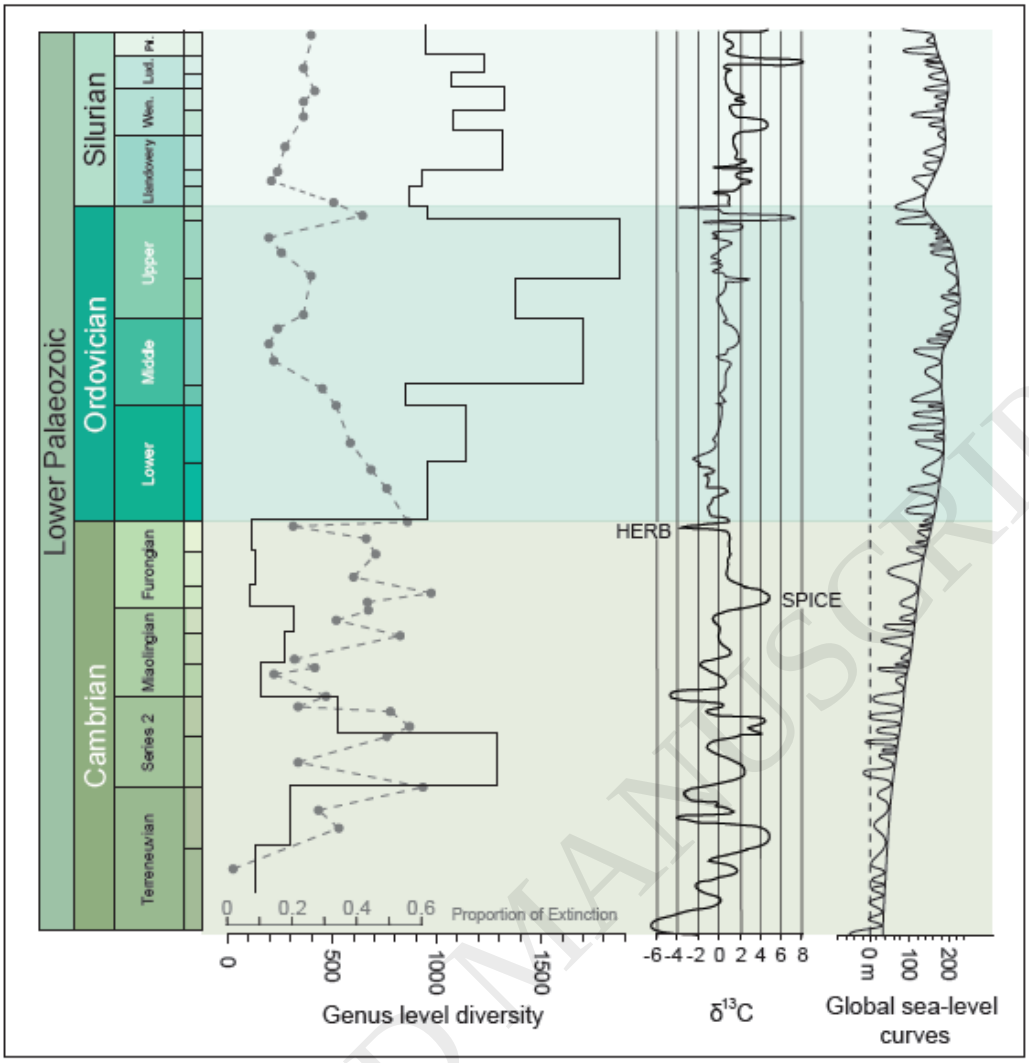

Table 1. Correlation analyses of raw and generalised-differenced (detrended) data of genus-level Cambrian–Silurian PBDB diversity. The relationship between the (total and the boundary-crossing, BC) observed and the sampled-in-bin (SIB) and the occurrence richness as a measure of sampling effort is tested. Both variables are analyzed per time unit. The parametric Pearson (r), and non-parametric Spearman (r_s) and Kendall (t) correlation tests were implemented. The corresponding correlation coefficients together with their associated probability values of no-correlation (p) are shown. * Significant values ($p < 0.01$). ** Highly significant values ($p < 0.001$).

Data analysis			Raw data						Detrended data					
			Pearson		Spearman		Kendall		Pearson		Spearman		Kendall	
	Dependent variable	Independent variable	r	p	r_s	p	t	p	r	p	r_s	p	t	p
1	Total diversity	SIB diversity	0.94^{**}	6.80×10^{-12}	0.97^{**}	7.41×10^{-7}	0.87^{**}	7.28×10^{-14}	0.97^{**}	1.55×10^{-14}	0.91^{**}	2.62×10^{-6}	0.79^{**}	5.26×10^{-10}
2	Total diversity	Nº of occurrences	0.85^{**}	5.43×10^{-8}	0.95^{**}	1.19×10^{-6}	0.83^{**}	8.60×10^{-12}	0.91^{**}	7.24×10^{-10}	0.84^{**}	2.06×10^{-6}	0.67^{**}	7.67×10^{-7}
3	BC diversity	SIB diversity	0.62^{*}	1.34×10^{-3}	0.70^{**}	1.22×10^{-4}	0.51	4.68×10^{-4}	0.49	1.75×10^{-2}	0.49	1.82×10^{-2}	0.34	2.19×10^{-2}
4	BC diversity	Nº of occurrences	0.50	1.30×10^{-2}	0.68^{**}	2.90×10^{-4}	0.48^{*}	1.15×10^{-3}	0.43	3.87×10^{-2}	0.39	6.73×10^{-2}	0.26	9.11×10^{-2}
5	SIB diversity	Nº of occurrences	0.94^{**}	2.23×10^{-12}	0.97^{**}	7.41×10^{-7}	0.90^{**}	2.67×10^{-15}	0.94^{**}	5.19×10^{-12}	0.94^{**}	2.13×10^{-6}	0.80^{**}	1.76×10^{-10}